ADDITIONAL FOSSILS IN DOMINICAN AMBER GIVE EVIDENCE OF ANTHER ABORTION IN MID-TERTIARY *TRICHILIA* (MELIACEAE)

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ABSTRACT

Three additional fossil flowers recovered from amber of the Dominican Republic, are similar in perianth shape, pubescence, staminal tube, and anther arrangement to 2 previously described *Trichilia* species from these deposits. Their androecia display variation in the degree of anther reduction in functionally pistillate flowers, leading to vestigial filaments and tiny, knob-like, non-functional anthers on the rim of the staminal tube. The 3 newly discovered flowers are illustrated to show features of perianth pubescence, anther development, and ovary pubescence characterizing the genus in these Mid-Tertiary tropical forest deposits. None of the newly found fossils is well enough preserved to allow an unequivocal placement within the earlier published species or to permit the description of separate taxa. The fossils indicate an early evolution of the unisexual flowers present in modern day dioecious and polygamous species of *Trichilia*.

RESUMEN

Tres flores fósiles adicionales recuperadas de ámbar de la Republica Dominicana, son similares en la forma del perianto, pubescencia, tubo estaminal, y colocación de las anteras a 2 especies de *Trichilia* descritas previamente de estos depósitos. Sus androceos muestran variación en el grado de reducción de las anteras en las flores funcionalmente pistiladas, dando lugar a filamentos vestigiales y anteras pequeñas como un nudo, no funcionales en el borde del tubo estaminal. Las 3 nuevas flores descubiertas se ilustran para mostrar las características de la pubescencia del perianto, desarrollo de la antera, y pubescencia del ovario que caracterizan a este género de depósitos de bosques tropicales del Terciario medio. Ninguno de los fósiles encontrados está lo suficientemente bien conservado como para permitir un emplazamiento inequívoco en alguna especie publicada previamente o para permitir la descripción de taxa diferentes. Los fosiles indican una evolución temprana de las flores unisexuales presentes actualmente en especies dioicas y polígamas de *Trichilia*.

INTRODUCTION

We recently described two new fossil species of *Trichilia* (Meliaceae) from Dominican amber, *T. antiqua* and *T. glaesaria* (Chambers et al. 2011). Since then, three additional pistillate flowers from the same deposits have been found in the Poinar amber collection at Oregon State University. These flowers show differing degrees of anther abortion and allow an improved interpretation of the earlier described taxa, integrating them into a gradient of anther reduction in the genus. In the original flower of *T. antiqua*, which had been browsed by an insect so that the pistil and one petal were missing, just one small, knob-like vestigial anther was present (op. cit., Fig. 5). We suggested that the other anthers might have been eaten by the insect; hence their functionality was unknown, and the gender of the flower could not be specified. One of the recently found specimens has at least 4 such knob-like anthers along with a number of missing anthers. It is not insect-damaged, therefore making clear that it and the fossil of *T. antiqua* are pistillate flowers displaying an extreme degree of anther reduction and loss.

Two other fossils illustrate nonfunctional anthers with much reduced locules, comparable to, or even smaller than, the anthers illustrated for *T. glaesaria* (op. cit., Fig. 1). Taken together, these fossils give evidence that in *Trichilia* species of that period, there was variation in anther development in pistillate flowers, ranging from nearly normal size to cases of missing or vestigial anthers. The nature of preservation of the 3 newer fossils obscures some other features necessary for a complete floral description. Despite their androecial variation, which in fact may be matched in some extant species (see below), it is not considered advisable to propose any new species based on the here described additional fossils.

MATERIALS AND METHODS

The fossils originated from mines in the Cordillera Septentrional of the Dominican Republic, between the cities of Puerto Plata and Santiago, island of Hispaniola. Two differing ages have been proposed for this amber deposit, the older being 45–30 Ma, based on fossil coccoliths (Cépek in Schlee 1999) and the younger being 20–14 Ma, based on foraminifera (Iturralde-Vinent & McPhee 1996). Most of the amber is secondarily deposited in turbiditic sandstones of the Upper Eocene to Lower Miocene Mamey Group (Draper et al. 1994). The specimens described here were found during a search of the Poinar amber collection for additional flowers of Meliaceae that might relate to those already described. They are designated as numbers D-9-27C, D-9-27D and D-9-27E in this collection. A newly described species of *Swietenia*, which incidentally had been illustrated earlier (Poinar & Poinar 1999), is also representative of fossil Meliaceae flowers in these amber deposits from the Dominican Mid-Tertiary tropical forest (Chambers & Poinar 2012).

RESULTS

The first illustrated flower, designated A (Figs. 1, 2) resembles *Trichilia glaesaria* in the shape and pubescence of its calyx and corolla (cf. Fig. 2 in Chambers et al. 2011). Its lobed, strigillose calyx differs from that of *T. antiqua*, which was described as glabrous and rotate. In apical view (Fig. 1), the ovary of flower A is well developed, 1 mm wide, strigillose, and situated at the base of the staminal tube. Four anthers can be seen, showing different degrees of extreme abortion. Three have knob-like terminal structures, which resemble the one much reduced anther seen in *A. antiqua* (op. cit., Fig. 5). A short filament is present on one of these (upper left arrow, Fig. 1), while the fourth remnant is a tiny filament with a mere suggestion of an anther (upper right arrow). Anthers are absent at other potential sites on the irregularly lobed, partly obscured staminal tube. On the evidence from this flower, the filament stubs of *T. antiqua* shown in Fig. 3 of Chambers et al. (op. cit.) might be reinterpreted as lacking anthers from the beginning, rather than having them removed earlier by an herbivorous insect.

In the flower designated B (Figs. 3, 4), the adaxial and abaxial sides of the petals are densely covered with shiny droplets of a glassy deposit, which obscures the natural pubescence of these surfaces. The calyx, barely in view, also has this deposit. In lateral view (Fig. 3), anthers with much reduced locules are visible in alternating higher and lower notches between acute lobes on the rim of the staminal tube. The apical view of this flower (Fig. 4) shows approximately 10 anthers, which are also covered with the glassy deposit. The stigma of the pistil is visible, but the ovary is too deeply placed to be characterized as to its pubescence or size.

The third flower, C, is illustrated in lateral view in Figure 5. Its calyx is not in view, and its petals are mostly too darkly stained to show the necessary details for a complete description. However, on the petal at the left (arrow), the abaxial surface can be seen to be strigillose, as was the abaxial petal surface in *T. glaesaria* (Chambers et al. 2011, Figs. 1, 2), and the petal at the right appears to have the papillate adaxial surface characteristic of flower A. At least 8 much reduced anthers are present on the rim of the staminal tube, in alternating higher and lower positions between acute lobes as in flower B, above, and in *T. glaesaria* (op. cit., Fig. 1). The locules of these anthers appear to be more reduced than in flower B. In an apical view of flower C (not shown), the ovary is glabrous, unlike that of flower A. It is interesting that in two extant *Trichilia* species, the ovary is glabrous before fertilization but develops pubescence afterward, as does the fruit (Pennington et al. 1981, p. 11). The intense staining of flower C does not allow further details to be observed. Flowers A and C differ greatly in anther development; however, as noted by an anonymous reviewer, "(t)he range of anther reduction between the 3 flowers described here could easily be found in a single modern day species."

DISCUSSION

The flowers under consideration here were not discovered until our earlier paper had been published. All 5 fossils are linked through their having been excavated from amber mines in the same ocean-deposited Mid-Tertiary strata, now uplifted in the Cordillera Central of Hispaniola. As discussed by Poinar and Poinar (1999), these amber deposits sample a characteristic Caribbean tropical forest over a span of many millennia, and it is

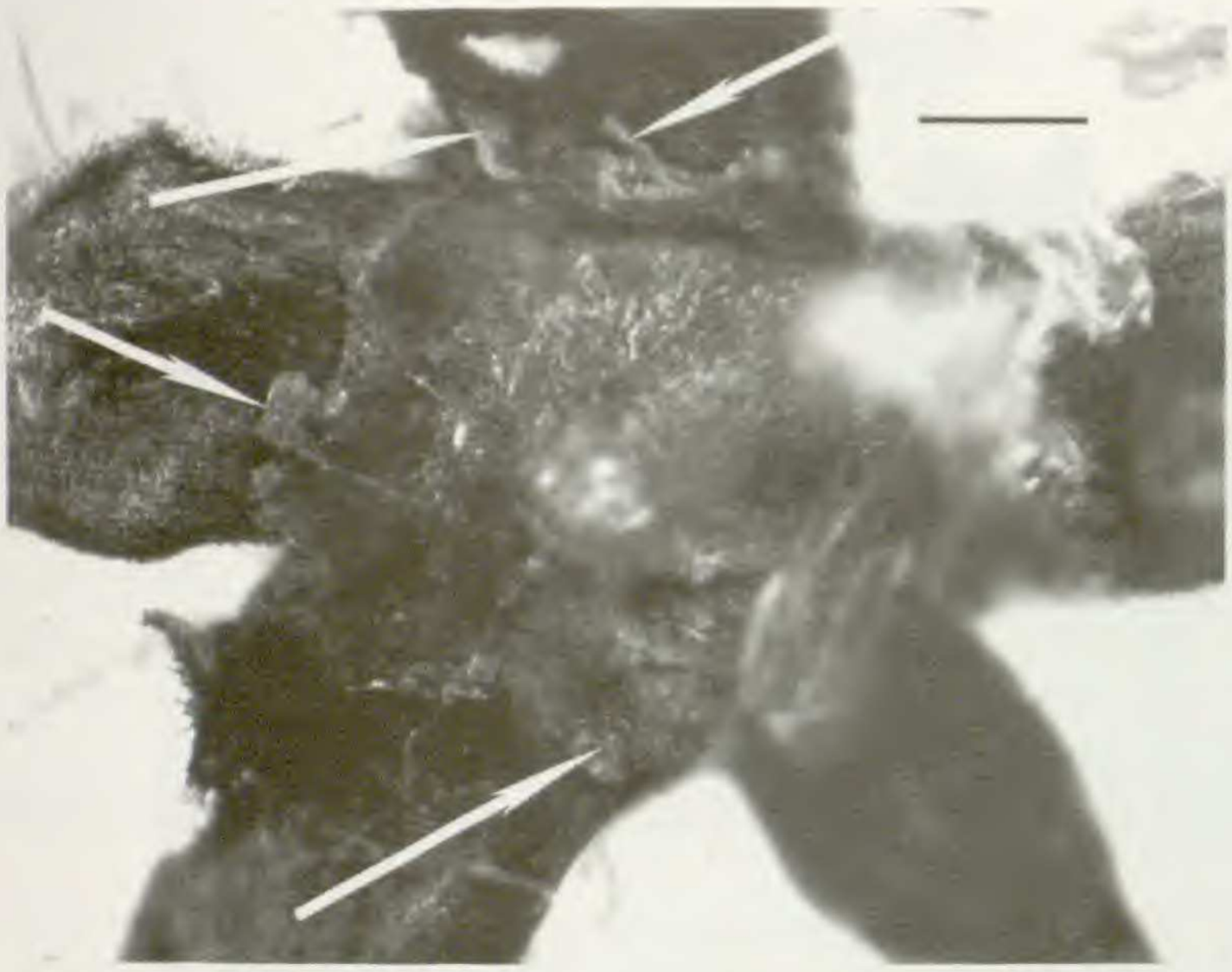

Fig. 1. *Trichilia* flower A, apical view. Arrows indicate 4 vestigial anthers. As far as can be seen, anthers are absent at other potential sites on rim of staminal tube. Bar = 0.86 mm.

Fig. 2. *Trichilia* flower A, lateral view. Note strigillose pubescence on abaxial surface of calyx and corolla. Bar = 0.48 mm.

possible that the *Trichilia* fossils described here do not represent contemporaneous species. What they illustrate is that *Trichilia* taxa in these forests were diverse in features such as perianth pubescence, pistil pubescence, and especially the nature of anther reduction and loss in pistillate flowers. However, lacking evidence relating to staminate flowers or to differences in the vegetative parts and inflorescence structure of the sampled taxa, we are limited as to any broad taxonomic conclusions that might be drawn from the observed variability in pistillate flowers. It is important, nevertheless, that these fossils be placed on record as part of the history of floral evolution in the genus, to be considered in possible future discussions of Meliaceae phylogeny.

The loss and extreme reduction of anthers in flower A, and probably also in *Trichilia antiqua*, goes beyond the description by Pennington et al. (1981) of androecia in functionally female flowers. These authors simply note (p. 26) that in *Trichilia* the "antherodes [are] narrower than anthers, not dehiscing, without pollen." In view of the review comments quoted above, this may be a generalization that omits a complete description of anther abortion and loss in modern species. That two of the Dominican fossils display such androecial reduction is evidence of its occurrence earlier in *Trichilia* floral evolution than might have been expected.

As discussed by Pennington et al. (1981), *Trichilia* is today the largest genus of Meliaceae in the New World, with ca. 85 species in lowland tropical America as well as ca. 14 species in Africa and 2 in the Indo-Malesian region. Its floral diversity, particularly in the androecium, well exceeds our sample of amber fossils (Pennington et al. op. cit., illustrations on pages 36–226). Respecting the age of *Trichilia*, Muellner et al. (2006) use evidence from known Meliaceae fossils, combined with chloroplast *rbcL* data, to estimate divergence times in the family. The DNA cladogram presented by these authors includes a monophyletic clade of *Trichilia* and 11 other genera, which is assigned an origin in the Oligocene. Apart from *Trichilia*, members of this clade are today limited to the Old World tropics, from Africa to Madagascar, India, Into-China, Malesia, and Austroasia. Muellner et al. (2006) propose a West Gondwanan Cretaceous origin for the family, followed by dispersal across Eurasia and between Eurasia and North America over the Beringian and North Atlantic land bridges. Further movement from North to South America occurred via island hopping and/or direct land connections during the Tertiary (see also Muellner et al. 2010, with a dense sampling of Cedreleae). As noted previously (Chambers et al. 2011), Pennington et al. (1981) recognized only two sections in *Trichilia*, Sect. *Trichilia* and Sect. *Moschoxylum* C. DC. The fossils discussed here are best placed in the emended Sect. *Moschoxylum*, the defining traits of which are the valvate petals and completely united filaments.

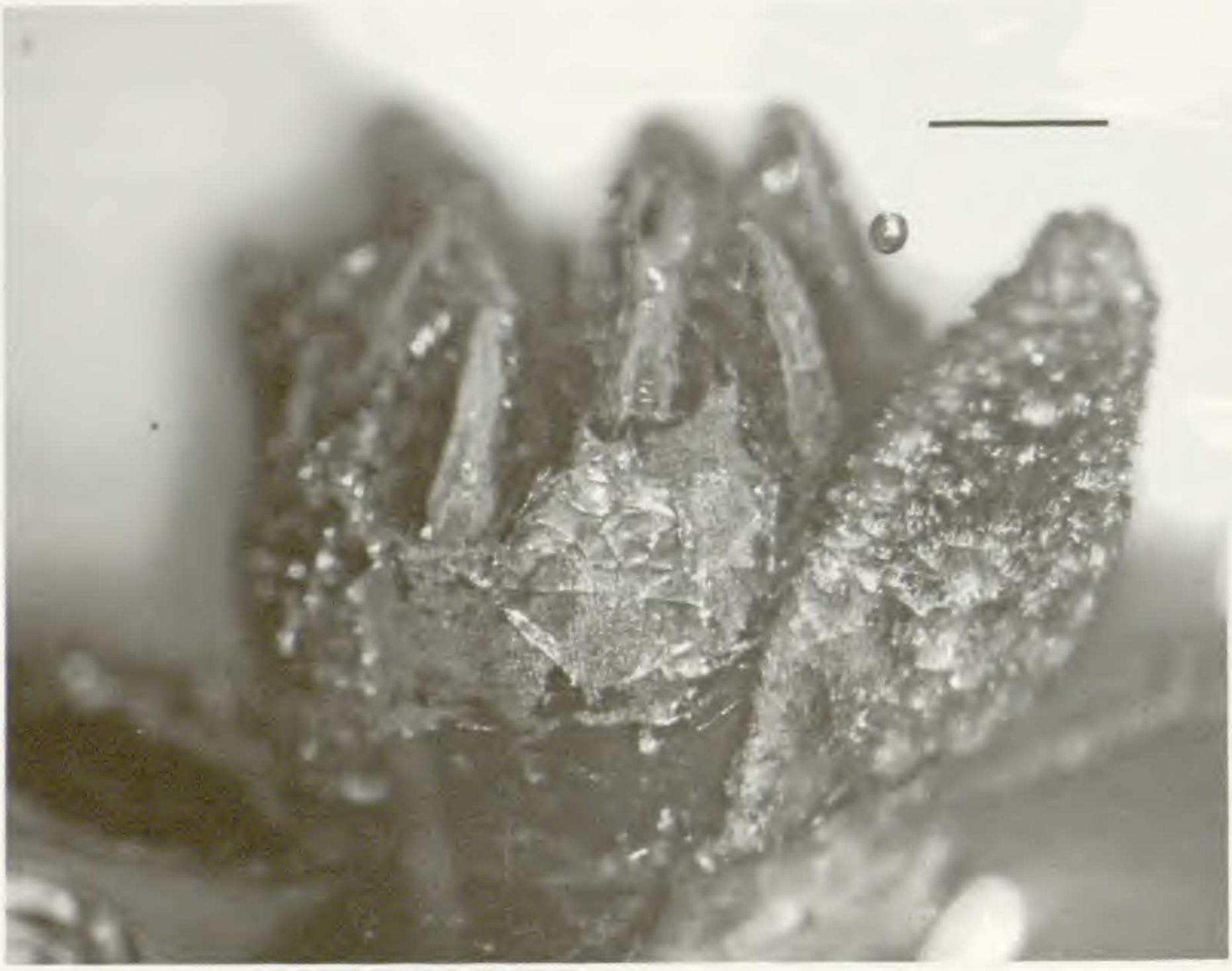

Fig. 3. *Trichilia* flower B, lateral view. Abortive anthers at higher and lower positions on rim of staminal tube. Bead-like deposits on perianth, formed during preservation, obscure surface features. Bar = 0.77 mm.

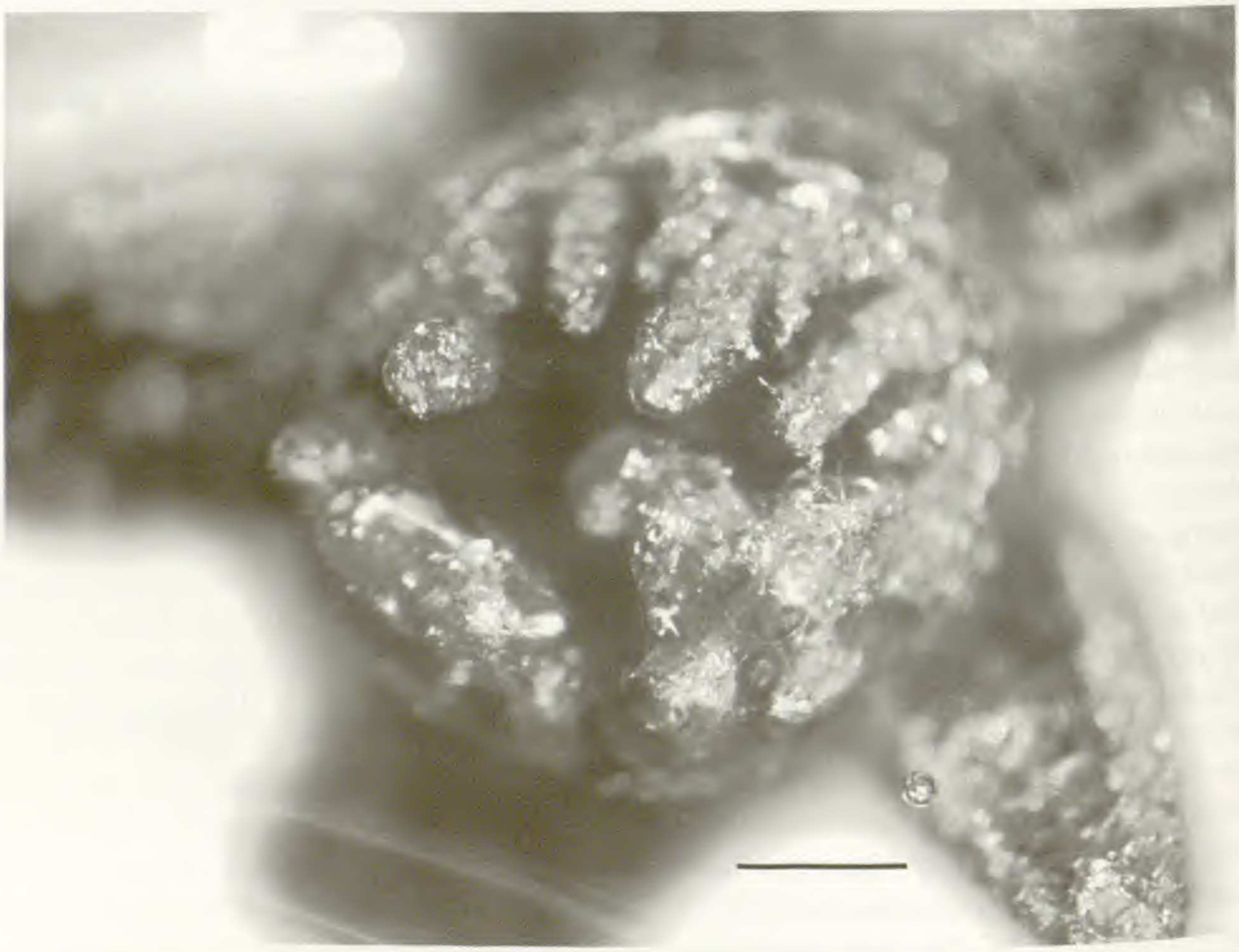

Fig. 4. *Trichilia* flower B, apical view. Stigma visible within filament tube. Bar = 0.80 mm.

Fig. 5. *Trichilia* flower C, lateral view. Note abortive anthers and strigillose abaxial surface of petal on left (arrow). Bar = 0.79 mm.

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